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Chromosomal analyses of Salticinae and Lyssomaninae reveal a broad occurrence of the 2n♂ = 28, X_1X_20 karyotype within Salticidae

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Abstract. Brazil possesses the richest fauna of Salticidae in the world, including 560 species; however, no representative of the Brazilian fauna has been cytogenetically analyzed up to now. It has been demonstrated that karyotype data are a useful source for discussions on the phylogeny and chromosome differentiation of some salticid lineages. In this work, the first chromosome study of salticid species from Brazil is presented, with the addition of five genera to the 38 previously investigated worldwide. The analysis of mitotic and/or meiotic cells revealed 2n♂ = 28, X_1X_20 in *Asaracus* sp., *Coryphasia* sp., *Chira* sp., *Frigga quintensis* (Tullgren, 1905), and *Lyssomanes pauper* Mello-Leitão, 1945. This karyotype constitution is the most common for Salticidae, occurring in species of distinct clades. The diploid number 2n♀ = 28 observed in *Hasarius adansoni* (Audouin, 1826) is unexpected, differing in one autosomal pair from the karyotype previously registered for males of the same species. The cytogenetic information reported here reinforces the wide occurence of 2n♂ = 28, X_1X_20 within Salticidae, including species belonging to different clades and biogeographical regions. This karyotype is a shared character of Salticidae + Philodromidae, found exclusively in these families within Dionycha, suggesting its sister relationship already proposed in the literature.

Keywords: Jumping spider, meiosis, sex chromosome system, diploid number, chromosome evolution

A hundred years has past since Painter (1914) cytogenetically studied a salticid spider for the first time, *Maevia inclemens* (Walckenaer, 1837) [under *Maevia vittata* (Hentz, 1846)]. Despite the huge contribution of Maddison (1982, 1996) and Maddison & Leduc-Robert (2013), which cytogenetically analyzed 86 salticids, only 155 species belonging to 38 genera were karyotyped up to now (Araujo et al. 2016). This number corresponds to only 2.65% of the 5,850 taxonomically described Salticidae species (World Spider Catalog 2016). Furthermore, many clades, mainly those predominantly composed of Neotropical speeies (Amycoida, Marpissoida, Euophryini and Freyina) or basal species (non-salticines) (Maddison 2015) remain almost unknown from the karyological point of view. Only six Neotropical Salticidae species, belonging to the genera *Bryantella* Chickering, 1946, *Dendryphantes* C.L. Koch, 1837, *Metaphidippus* F.O.Pickard-Cambridge, 1901 (Salticinae, Dendryphantini, Dendryphantina) (Scioseia 1997) and *Habronattus* F.O.Pickard-Cambridge, 1901 (Salticinae, Plexippini, Harmochirina) (Maddison & Leduc-Robert 2013) were cytogenetically studied, and, among these genera, only *Bryantella* is exclusively Neotropical (World Spider Catalog 2016). Within non-salticines, only *Holcolaetis vellerea* Simon, 1910 (under *Holcolaetis vidua* Lessert, 1927) (Spartaeinae, Spartaeini, Holcolaetina) was karyotyped (Mittal 1961, 1964).

At a first glance, the salticids cytogenetically analyzed seem to constitute a relatively homogeneous group, mostly composed of species with 2n♂ = 28, X_1X_20 (Araujo et al. 2016). A multiple sex chromosome system (SCS) of the X_1X_20 type is rare in other animal groups but the most common in spiders (see Araujo et al. 2012). In this SCS, the sex is not determinate by the presence of an Y or W chromosome, as it occurs in most mammals and birds. The number of copies of each X chromosome determines the sex, a single copy of each one (X_1X_20) is characteristic of a male and two copies of each one ($X_1X_1X_2X_2$), characterizes a female. The "0" after the X_1X_2 denotes the absence of a Y chromosome in male complement. Thus, in this SCS, if the male diploid number is 2n♂ = 28 (26 autosomes plus X_1X_2), the female diploid number is 2n♀ = 30 (26 autosomes plus $X_1X_1X_2X_2$). At the end of male meiosis I, both X_1 and X_2 segregate to the same cell pole and the opposite pole contains no sex chromosomes. Recently, a study showed that uncommon karyotypes in spiders, with a multiple sex chromosome system including a Y chromosome (X_1X_2Y and $X_1X_2X_3Y$), occur in *Habronattus*, and probably evolved independently several times within this genus (Maddison & Leduc-Robert 2013).

Cytogenetic studies on underrepresented salticid clades could provide us with information about the homogeneity or heterogeneity of some lineages and could be useful for discussions concerning salticid systematics. Thus, the goal of this study is to analyze the chromosomes of six Salticidae species from Brazil: the Salticinae *Asaracus* sp., *Chira* sp. and *Frigga quintensis* (Tullgren, 1905) (Aelurillini), *Coryphasia* sp. (Euophryini), and *Hasarius adansoni* (Audouin, 1826) (Hasar-

Table 1.—Salticid spiders investigated in this work with their respective samples and collection localities in Brazil. SP = state of São Paulo, MS = state of Mato Grosso do Sul, PR = state of Paraná. Classification according to Maddison (2015).

Taxa	Sample	Collection locality
Salticinae, Saltafresia, Aelurillini, Freyina		
Asaracus sp.	1♂	Margem da Lagoa Xambrê, Parque Nacional de Ilha Grande, Altônia (23°52′21″S, 54°00′01″W), PR
Chira sp.	1♂	Rio Claro (22°24′00″S, 47°34′19″W), SP
Frigga quintensis (Tullgren, 1905)	2♂	Margem da Lagoa Xambrê, Parque Nacional de Ilha Grande, Altônia (23°52′21″S, 54°00′01″W), PR; Ivinhema (22°18′00″S, 53°49′16″W), MS
Salticinae, Saltafresia, Euophryini		
Coryphasia sp.	1♂	Rio Claro (22°24′00″S, 47°34′19″W), SP
Salticinae, Saltafresia, Hasariini		
Hasarius adansoni (Audouin, 1826)	1♀	Ivinhema (22°18′00″S, 53°49′16″W), MS
Lyssomaninae		
Lyssomanes pauper Mello-Leitão, 1945	4♂,3♀	Reserva Particular do Patrimônio Natural da UFMS (20°29′58″S, 54°36′48″W), Campo Grande, MS

iini), and the Lyssomaninae *Lyssomanes pauper* Mello-Leitão, 1945.

Except for the genus *Hasarius* Simon, 1871, karyotyped by Suzuki (1951, 1954), the remaining genera were not previously cytogenetically analyzed (Araujo et al. 2016).

METHODS

The number of individuals and collection localities of the species examined in this work are listed in Table 1. Collecting permits were provided by the Instituto Brasileiro do Meio Ambiente e dos Recursos Renováveis – IBAMA and Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio (15382-1 and 15157-1). The voucher specimens were deposited in the arachnologieal eollection of the Laboratório Especial de Coleções Zoológicas, Instituto Butantan (IBSP, curator A. D. Brescovit), São Paulo, state of São Paulo, Brazil. The chromosome preparations were obtained following Araujo et al. (2008), i.e., the gonads were submitted to 2 hours in a treatment with 0.16% colchicine solution (diluted on physiologic solution: 7.5 g NaCl, 2.38 g Na_2HPO_4, 2.72 g KH_2PO_4, in 1 l of distilled water), 15 minutes in a hypotonic treatment with tap water, and fixation with methanol/acetic acid (3:1). Later, the gonads were dissociated in 45% acid acetie solution on the surface of a microscope slide that was heated to 35 °C/ 40 °C, and standard stained with 3% Giemsa solution (3% of commercial Giemsa and 3% of phosphate buffer pH 6.8 in distilled water) for 12 min. At least 30 cells were considered in the analysis of each species. The chromosome morphology was determined following the nomenclature proposed by Levan et al. (1964). Difficulties in obtaining certain stages of cell division occurred due to the low number of specimens, for most species, or the development stage of the individuals, as in the case of *L. pauper*.

RESULTS

Male diplotene/metaphase I cells of *Asaracus* sp., *Coryphasia* sp., *Chira* sp. and *F. quintensis* are composed of 13 autosomal bivalents and two sex univalents (X_1 and X_2). Thus, the meiotic formula of these species is $13II+X_1X_20$. The number of chiasmata per bivalent is usually one, localized on terminal, interstitial or proximal regions, but some bivalents with two terminal chiasmata can be observed in some cells. The sex chromosomes can be easily identified due to their positive heteropycnosis and/or peculiar disposition, since they normally appear side by side or at least close to each other (Fig. 1A–D). The positive heteropycnosis of the sex chromosomes is detected even at pachytene, in which it is possible to observe the X_1 and X_2 closely packed, being difficult to establish their limits (Fig. 1E), or clearly separated from each other (Fig. 1F). Male metaphase II cells of *Asaracus* sp. and *F. quintensis* exhibited n = 13 or n = 15, confirming the regular segregation of the X_1 and X_2 chromosomes to the same pole at anaphase I (Fig. 1G, H). In some metaphase II nuclei, the sex chromosomes cannot be distinguished from the autosomes (Fig. 1G), but in others, these elements presented a positive heteropyenosis (Fig. 1H).

Spermatogonial prometaphase/metaphase cells of *Coryphasia* sp., *F. quintensis* and *L. pauper* showed $2n♂ = 28$, X_1X_20 (Fig. 1I, K), which is compatible with the meiotic findings and allow us to conclude that all salticid species above mentioned possesses $2n = 28$, X_1X_20 in males and $2n = 30$, $X_1X_1X_2X_2$ in females. Unfortunately, only female specimens of *H. adansoni* were collected. The analysis of oogonial metaphases of *L. pauper* and *H. adansoni* revealed the diploid number of 2n = 30 and 2n = 28, respectively (Fig. 1L, M). The chromosomal morphology was not established due to the irregular shape of the elements and/or absence of mitotic plates, except for the chromosomes of *L. pauper* and *H. adansoni*, which are clearly telocentrics.

DISCUSSION

The data presented in this work are the first for salticid species collected in Brazil. This seems to be fundamental considering that Maddison & Hedin (2003) and Maddison et al. (2008) suggest a biogeographical division between Old World and New World salticid fauna. In addition, almost all new world salticids cytogenetically analyzed are from North America (Pinter & Walters 1971; Maddison 1982, 1996; Tugmon et al. 1990; Maddison & Leduc-Robert 2013), despite the fact that Brazil possesses the richest salticid fauna in the world, with 560 species (Metzner 2016). All Salticidae species analyzed here, except *H. adansoni*, revealed meiotic and/or mitotic features that are consistent with $2n♂ = 28$, X_1X_20, the

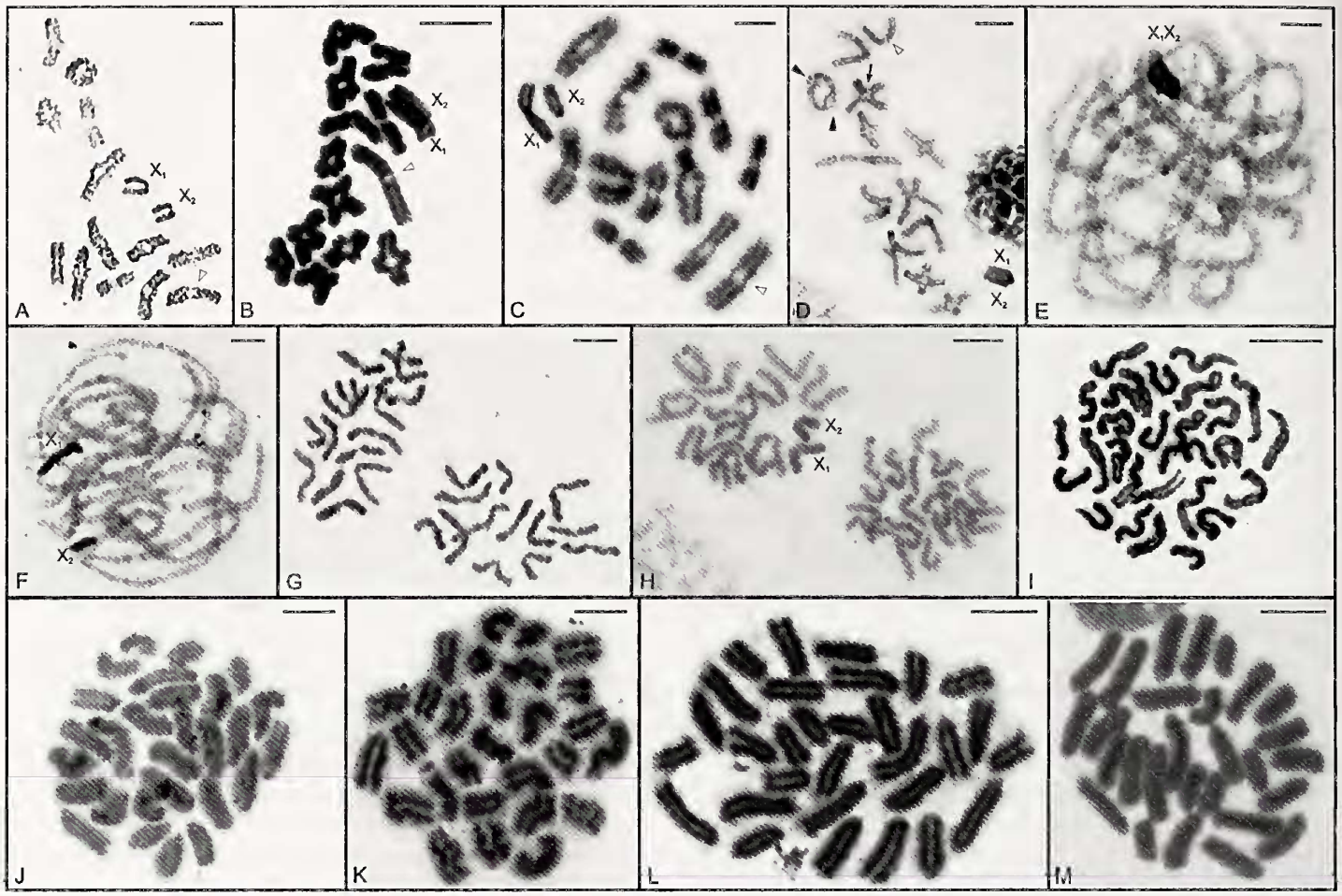

Figure 1.—Meiotic and mitotic cells of the salticid species. A–D. Diplotene/metaphase I spermatocytes of *Asaracus* sp. (A), *Coryphasia* sp. (B), *Chira* sp. (C) and *Frigga quintensis* (D) with 13 autosomal bivalents plus two sex univalents (X_1 and X_2). For exemplification, the arrow indicates one autosomal bivalents with one interstitial chiasma, the empty arrowheads show autosomal bivalents with one terminal chiasma, and the full arrowheads point to two terminal chiasmata in one autosomal bivalent. E, F. Pachytene cells of *Chira* sp., showing the positive heteropycnosis of the sex chromosomes, that appear together (E) or separated (F). G, H. Metaphase II cells of *Asaracus* sp. (G) and *Frigga quintensis* (H) with n = 13 in the right and n = 13 + X_1X_2 in the left. In (H) it is possible to identify the positive heteropycnotic sex chromosomes. I–K. Spermatogonial prometaphase/metaphase cells of *Coryphasia* sp. (I), *Frigga quintensis* (J), and *Lyssomanes pauper* (K), with 2n♂ = 28. L, M. Oogonial metaphase cells of *Lyssomanes pauper* (L), with 2n♀ = 30 and *Hasarius adansoni* (M), with 2n♀ = 28. Scale = 10 μm.

most common chromosome constitution observed in the family (Araujo et al. 2016).

Despite the fact that no quantitative analysis of chiasmata was carried out, the species analyzed here seem to show a tendency to have only one chiasma per bivalent, a common characteristic in spiders (White 1973). However, in contrast to the observations of White (1973) suggesting that the chiasmata are primarily proximal in spiders, the nuclei of the species analyzed herein show a diversity of chiasma position (distal, interstitial and proximal). This pattern was already described for *Habronattus* species with a X_1X_20 system, contrasting to the Y-possessing species of the same genus, which showed a tendency to have distal chiasmata (Maddison & Leduc-Robert 2013). Chiasmata in other positions than distal could act against the occurrence of chromosome fusions that form metacentric elements, including metacentric neo-Ys (for a more detailed discussion see White 1973 and Maddison & Leduc-Robert 2013).

Based on our results, *Asaracus*, *Chira* and *Frigga* (2n♂ = 28, X_1X_20) are the only genera, along with *Aelurillus* Simon, 1884, with described karyotypes within the tribe Aelurillini (Maddison 2015).The karyotype data of *Aelurillus politiventris* (O. P-Cambridge, 1872), from Israel, is 2n♂ = 21, X0 (Gorlova et al. 1997). This difference in diploid number and sex chromosome system can reflect the biogeographical distribution of these genera. Instead of belonging to the same tribe Aelurillini, the first three genera are part of the Neotropical subtribe Freyina, and *Aelurillus* belongs to the Afro-Eurasian subtribe Aelurillina (Maddison 2015). Thus, within Aelurillini, the karyotype seems to be subtribe-specific, but it is important to emphasize that most genera, including the entire African subtribe Thiratoscirtina, are cytogenetically unknown.

Euophryini, which encompasses *Coryphasia* (Maddison 2015), possesses two other species that were cytogenetically studied: *Euophrys pseudogambosa* Strand, 1915, from Israel (Gorlova et al. 1997) and *Jotus minutus* L. Koch, 1881 (Suzuki 1951), both also with 2n♂ = 28, X_1X_20. In the phylogenetic

hypothesis of Zhang & Maddison (2015), *Coryphasia*, *Euophrys* C.L. Koch, 1834 and *Jotus* L. Koch, 1881 belong to distinct clades within Euophryinae (currently Euophryini, see Maddison 2015). However, despite the phylogenetic and geographical distance, all three genera share the same diploid number and sex chromosome system. *Neon* Simon, 1876, classically placed in Euophryinae (Prószyński 2012; Metzner 2016), was relocated to a new group, Astioida, by Maddison et al. (2008, 2014), which possesses only one cytogenetically analyzed genus, *Myrmarachne* MacLeay, 1839. A close relationship between *Neon* (Astioida, Neonini) and *Myrmarachne* (Astioida, Myrmarachnini) is proposed by the cytogenetic data, because *Neon reticulatus* (Blackwall, 1853), from Turkey, exhibits 2n♂ = 21, X0 (Kumbıçak 2014) and four of the six *Myrmarachne* species analyzed cytogenetically showed 2n♂ = 23, X0 (Hackman 1948; Bole-Gowda 1958); these karyotypes are much more similar to each other than to the 2n♂ = 28, X_1X_20 found in the Euophryini *Coryphasia*, *Euophrys* and *Jotus*.

Some considerations should be addressed regarding the female speeimen of *H. adansoni* (Hasariini) with the unexpeeted 2n♀ = 28. . Taking into account that Suzuki (1954) described 2n♂ = 28, X_1X_20 in *H. adansoni*, it was supposed that females of this species would have a diploid number of 2n♀ = 30, $X_1X_1X_2X_2$. However, this female specimen has a diploid number lower than the expected. Even though the sex chromosome system was not identified in the present work, if we consider the same system found by Suzuki (1954), the female specimen analyzed here probably has the constitution 2n♀ = 28, $X_1X_1X_2X_2$. Thus, this could be a case of polymorphism in the number of autosomes, that is, 26 autosomes in the Japanese population studied by Suzuki (1954) and 24 autosomes in the population from Ivinhema, state of Mato Grosso do Sul, Brazil (present work). Polymorphism in the number of autosomes was already described in another salticid species, *Habronattus viridipes* (Hentz, 1846), in which Maddison (1982) found 2n♂ = 28, X_1X_20 in most males, and 2n♂ = 30, X_1X_20 in only one specimen. Both cases, show a discrepant chromosome number in only one specimen. Nevertheless, the presence of this unusual diploid number within the *H. adansoni* population from Ivinhema, Brazil, needs still to be confirmed. Without a more thorough collection effort, a distinction between a population polymorphism (Japan x Brazil) or an individual chromosome variation eannot be made. In fact, the 2n♂ = 28, X_1X_20 observed in other eytogenetically analyzed Hasariini, *Habrocestum rubroclypeatum* Lessert, 1927 (Mittal, 1964), reinforces the hypothesis that the 2n♀ = 28 encountered in the female specimen of *H. adansoni* from Ivinhema is a populational variation of the karyotype 2n♂ = 28/2n♀ = 30, which is commonly described for Salticidae.

Lyssomanes pauper is the first Lyssomaninae karyotyped, but the occurrence of 2n♂ = 28, X_1X_20 in this species and the other non-salticine cytogenetically studied, *Holcolaetis vellerea* (Mittal 1961, 1964) (Spartaeinae, Spartaeini), both basal salticids, points to a broad distribution of this karyotype within salticids. Moreover, the presence of 2n♂ = 28, X_1X_20 only known for Salticidae and Philodromidae within Dionyeha (see Araujo et al. 2016), suggests a sister relationship between these families, as already proposed by Ramírez (2014).

The data presented here reinforce the karyotypic homogeneity within salticids, with the 2n♂ = 28, X_1X_20 widespread in species of several clades and biogeographical regions. However, in many clades, only one or a few species were karyotyped so far, a situation that blurs an unrevealed chromosome heterogeneity, as shown for *Habronattus*, a genus that has around 66% of its 99 species already karyotyped (Araujo et al. 2016; World Spider Catalog 2016). This genus exhibited four different diploid complements, including the X_1X_2Y, $X_1X_2X_3Y$ and X0 sex chromosome systems, besides the classical 2n♂ = 28, X_1X_20 (Maddison & Leduc-Robert 2013).

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